An occasional review

Adaptive response of mammalian skeletal muscle to exercise with high loads

M. J. N. McDonagh and C. T. M. Davies
MRC Muscle Group, Department of Physiology and Pharmacology, Queen's Medical Centre, Nottingham

Key words: Muscle – Exercise – Training – Strength – Hypertrophy – Contractions

I Introduction

This review is concerned with the effects on muscle of chronic exercise using high loads. An attempt is made to assess the nature of the training stimulus, the rate of response of the tissue to the stimulus and the underlying biochemical and neurological mechanisms of the response.

In order to clarify the later discussion it is useful here to begin with a few operational definitions. A muscle generates ‘force’ when it attempts to accelerate a load or some other form of resistance. The term ‘load’ refers to the mass moved during a single contraction and ‘work’ has its usual physical meaning. Active use of energy by a muscle is usually referred to as a ‘contraction’ even if no actual contraction of muscle length occurs.

Two main types of muscle contractions are commonly distinguished. In ‘isometric’ or ‘static’ contractions, muscle force is developed at a constant muscle length. In ‘dynamic’ contractions muscle shortening (‘concentric’ contraction) or lengthening (‘eccentric’ contraction) occurs. Dynamic contractions are usually termed ‘isotonic’ if the load is preset and the velocity of the contraction measured, and ‘isokinetic’ if the velocity is preset and the load measured.

Under isotonic conditions involving the lifting of weights, a rough estimate of strength is the weight which can be lifted by a particular muscle group once only without a rest. For the purposes of this review the ‘strength’ of a particular muscle group is defined as the force of a 2–5 s maximal voluntary isometric contraction or ‘M.V.C.’.

Following this introduction, Part II describes the known effects on muscle force of training using voluntary isometric and isotonic contractions against high resistance. The response of voluntary and electrically evoked forces are both considered. In Part III the adaptation of muscle force to electrical stimulation is covered. The first section of Part IV examines the effect of training on the hypertrophy of whole muscles and of particular fibre types. The second section reviews the current theories about the underlying biochemical processes triggering hypertrophy. The role of neural learning in determining maximal voluntary force is considered in Part V.

Throughout the review, data from both human and animal muscle experiments are included. This reflects the belief of the reviewers that both approaches are essential to an understanding of the adaptive response of mammalian muscle to chronic exercise with high loads.

II Training using voluntary contractions

A. Effects on maximum voluntary force

I. Isometric training. A renewed interest in isometric training was aroused by a series of experiments conducted by Hettinger and Muller in the 1950’s and summarised by Hettinger (1961). In these experiments they tried to elucidate the optimal regime for producing an increase in strength. They suggested that the maximum gains in strength (e.g., 2% per week for the elbow flexors) were produced by one 4–6 s contraction per day at a force of 40–50% of maximum. It was suggested that longer, stronger and more frequent contractions did not increase strength gains. These results have remained controversial for two main reasons. Firstly, in subsequent publications...
from these authors, the strength gains per week have been revised downwards and the exercise required to produce them revised upwards (Royce 1964). Secondly, other authors have not been able to substantiate Hettinger and Muller's earliest results. For example, Bonde-Petersen (1960) found that one maximal 5 s isometric contraction per day of the elbow flexors, 4 days a week for 36 training days, produced no significant increase in strength, whereas 10 contractions per day produced a 16% increase.

It is generally accepted but perhaps not fully substantiated that training with maximal isometric contractions is more effective than training with submaximal contractions. However, it has been reported that seven daily contractions, equal to 30% of maximum, produced an improvement in maximal voluntary force after 6 weeks (Davies and Young 1983). The contractions were held for the unusually long time of 60 s and were slightly less effective than training using maximal 3 s contractions. Most workers have used maximal isometric contractions in training regimes designed to increase strength.

Table 1 summarises some of these experiments. In order to compare the effectiveness of each regime the increase in force has been expressed as a percentage increase per training day (column 7). The gains in strength range from 0.4 to 1.1% per day. It is not known if this rate of increase represents the maximum which is physiologically possible.

Other factors as well as force may influence the effectiveness of a training regime. Both duration (column 2) and number of contractions (column 3) may be related to the rate of increase of strength. The data in Table 1 suggest that one contraction per day is not sufficient to produce a training effect, whereas five or more contractions per day are effective. Using this tabulated data, the duration of the contraction shows a poor correlation with rate of strength increase ($r = 0.0015$ NS). The number of contractions per day shows a correlation of $+0.635$ (NS) with rate of strength increase and the product: duration of contraction $\times$ contractions per day a correlation of $+0.694$ ($P < 0.05$) with this variable.

On the basis of all these considerations, the most effective isometric training regime would seem to be one in which maximal contractions are used and in which the product of contraction duration $\times$ number of contractions per day is large. Such a regime produces a gain in isometric strength of 1% per day. The physiological basis of the efficacy of this training regime is probably as follows: motor units are recruited in a fixed order according to the level of force required from the whole muscle (Milner-Brown et al. 1973). This means that usually only in very strong contractions are the high threshold motor units fully recruited and fully activated and hence subjected to a training stimulus. However, it should be noted that in submaximal contractions of long duration these high threshold units may be recruited by the nervous system in an effort to maintain force against fatigue. This may explain the efficacy of the 30% contractions found by Davies and Young (1983). Frequent recruitment of high threshold motor units is probably necessary both to learn more efficient patterns of neural control (see Section V) and to activate protein synthesis in the fibres comprising these units (see Section IV).

### Table 1. The effect of training using maximal voluntary isometric contractions on M.V.C.

<table>
<thead>
<tr>
<th>Author</th>
<th>Duration of contraction/s</th>
<th>Contraction/ day</th>
<th>Product Col. 1 $\times$ Col. 2</th>
<th>Number of training days</th>
<th>M.V.C. increase (%)</th>
<th>M.V.C. % day</th>
<th>Muscles</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ikkai and Fukunaga 1970</td>
<td>10</td>
<td>3</td>
<td>30</td>
<td>100</td>
<td>92</td>
<td>0.9</td>
<td>Elbow flexors</td>
</tr>
<tr>
<td>Komi et al. 1978</td>
<td>3–5</td>
<td>5</td>
<td>15–25</td>
<td>48</td>
<td>20</td>
<td>0.4</td>
<td>Quadriceps</td>
</tr>
<tr>
<td>Bonde-Petersen 1960</td>
<td>5</td>
<td>10</td>
<td>50</td>
<td>36</td>
<td>16</td>
<td>0.4</td>
<td>Elbow flexors</td>
</tr>
<tr>
<td>Bonde-Petersen 1960</td>
<td>5</td>
<td>1</td>
<td>5</td>
<td>5</td>
<td>8</td>
<td>0</td>
<td>Elbow flexors</td>
</tr>
<tr>
<td>Davies and Young 1983</td>
<td>3</td>
<td>42</td>
<td>126</td>
<td>35</td>
<td>30</td>
<td>0.86</td>
<td>Triceps surae</td>
</tr>
<tr>
<td>McDonagh et al. 1983</td>
<td>3</td>
<td>30</td>
<td>90</td>
<td>28</td>
<td>20</td>
<td>0.71</td>
<td>Elbow flexors</td>
</tr>
<tr>
<td>Grimby et al. 1973</td>
<td>3</td>
<td>5</td>
<td>90</td>
<td>30</td>
<td>32</td>
<td>1.1</td>
<td>Triceps</td>
</tr>
</tbody>
</table>

Col. 5 No. days on which training was actually performed

Col. 6 $M.V.C.\ increase = \frac{\text{Post-training force} - \text{pre-training force}}{\text{pre-training force}} \times 100$

Col. 7 $M.V.C.\ %\ day = \frac{M.V.C.\ increase\ %}{\text{no. of training days}}$